Understanding spatially explicit capture-recapture parameters for informing invasive animal management

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Abstract

Spatially explicit capture-recapture modelling is used to estimate population density to enhance our ecological understanding and management of wildlife populations. The two primary parameters estimated in the capture process of these models are σ and g_0. The σ parameter is the standard deviation of a bivariate normal home range kernel (indicating home range size), while g_0 is the probability of capture by a device placed at the home range center. These parameters are being increasingly generalized and used in simulation models to predict detection or capture rates of invasive animals to inform management strategies. Given the sensitivity of simulation model predictions to parameter values, we undertook an analysis of pre-existing GPS telemetry and trapping data of invasive brushtail possums (*Trichosurus vulpecula*) across New Zealand to address the following three questions. First, how does σ vary with population density, habitat, and age-sex class? Second, how is g_0 influenced by home range size (i.e., σ) and trap type? Third, how much does the predicted probability of capture or detection of individuals vary within and across sites? We used data from 180 possums across 18 sites to develop a Bayesian hierarchical model. Results showed that σ decreased with increasing population density and increasing farm area. Juveniles and males tended to have larger home ranges (higher sigma parameters) than adults and females. There was a strong negative relationship between σ and g_0, and g_0 was highest for cage traps and lowest for raised leg-hold traps. Despite the potential compensatory inverse effect of g_0 with σ, the probability of capturing a randomly located possum by a large array of traps increased with increasing σ. Results show that selection of σ for predictive simulation modelling should begin with an estimated or assumed population density. The associated g_0 should then be identified as a function of σ, and stochasticity should be incorporated to account for inter-individual variability

Keywords: Bayesian; capture; detection; eradication; hierarchical model; simulation; *Trichosurus vulpecula*

Introduction

Spatially explicit capture-recapture modelling has the primary ecological objective of estimating population density in a particular area (**????**). These models have been extended to estimate population growth rates and immigration (**??**). The two primary parameters estimated in the detection or capture process of these models (i.e., g_0 and σ; see below) are being increasingly generalized and used in simulation models to predict detection or capture rates of a specified surveillance or trapping regime. This has the potential to *a priori* significantly improve survey design or the efficiency of management interventions (**?**).

The spatially explicit detection models commonly assume a symmetrical bivariate normal home range using a half-normal detection function, but other functions are available (**??**). The first parameter influencing detection is the probability of capture of a given animal over a set period (e.g., one night) when the device is located at the animal's home range center (**??**). This usually corresponds to the maximum probability of capture. The second parameter, σ, is the standard deviation of a bivariate normal home range kernel, which determines the rate of decay in the probability of detection with increasing distance between the home range center and the detection device. Using assumed values or distributions of these two parameters, based on empirical estimates, one can quantify the probability of detecting or capturing an individual animal or a group of animals and identify the optimal device deployment strategy that is most likely to deliver desired research or management outcomes (e.g., **?**).

Invasive species are well recognized as a threat to the integrity of natural biodiversity, ecosystem

56 function and services, and primary productivity (**??????**). Spatially explicit agent-based

57 simulation models using g_0 and σ are being used to estimate the control effort and management

58 conditions required to achieve population-suppression objectives or the feasibility of eradication

59 (**???**). Agent-based models also use these parameters to explore how distracting odors can be

60 deployed to lure invasive predators away from endangered prey (**?**). Given the high financial

61 expenditures required in perpetuity to minimize impacts of invasive species (**?**), eradication is

62 becoming an increasingly attractive strategy which potentially can deliver high ecological

63 benefits (**???**). Eradication programs can benefit from exploring trapping simulation models

64 early-on, which incorporate g_0 and σ estimates, to assess the cost-effectiveness of alternative

65 trapping regimes in achieving zero pest densities. At the latter stages of the program, g_0 and σ

66 estimates can be incorporated in surveillance data models to quantify the probability that

67 eradication has been successfully achieved given no recent detections (**????**).

68 As described above, trapping and surveillance simulation models can and have become an

69 integral tool in the invasive species management decision support toolbox. However, given the

70 sensitivity of model predictions to parameter values, it is important to have accurate estimates for

71 simulation experiments to ensure effective research design or management outcomes. The g_0 and

72 σ parameters have largely been treated independently in simulation modelling conducted thus far,

73 however, there is a clear inverse relationship (**?**) that requires further analysis. For example, it is

74 expected that an animal with a comparatively large home range (i.e., σ) will spend less time

75 around the home range center, and this should be reflected in a smaller g_0. The exact shape of this

76 inverse relationship is uncertain. To accurately simulate detection dynamics within a given

77 research or management site, a quantitative method is required for estimating the mean and

78 variance of σ within a population, and a corresponding model for predicting g_0. The σ parameter

79 may vary with age and sex of individuals, habitat and population density (**???????**). Given the

80 expected variation in σ due to population density and habitat, it would be inappropriate to

81 generalise a single combination of parameters across diverse sites.

82 In this study we developed a spatially explicit capture recapture model using trapping and GPS

83 telemetry data on 180 brushtail possums (*Trichosurus vulpecula*) across 18 sites in New Zealand.

84 Possums are native to Australia but are an invasive species in New Zealand. We used this model

85 to estimate population density, σ and g_0, and addressed the following three questions. First, how

86 does σ vary with population density, habitat, and age-sex class? Second, how is g_0 influenced by

87 home range size (i.e., σ) and trap type? Third, how does the predicted probability of capture or

88 detection of individuals vary with σ, different trap types and trap densities. The last question

89 addresses the practical importance for the interacting dynamics among habitat, density, σ and g_0

90 for detecting and trapping animals on landscapes. Understanding the relationship among these

91 parameters and how they are influenced by environmental, demographic and technical factors will

92 help guide their empirical parameterisation, and how they are used in simulation models to

93 identify optimal management strategies for diverse invasive species.

Methods

Data

96 We analyzed GPS telemetry data collected in nine previously conducted studies, which included

97 180 possums from 18 different sites (Table **??**). The scheduled frequencies for obtaining location

98 data across sites were generally 4 fixes per night at 2-hour intervals (see details on individual

99 possums in Table S1 in Supplemental Material). The population density was expected to vary

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100 across sites because of different levels and frequency of population control and habitat, which was

101 categorized as forest, grassland or scrub. Forests were characterized by dominant tree cover by

102 indigenous and exotic species. Grassland was native and exotic grasslands (including productive

103 livestock grazing areas). Scrub was primarily covered by native tussocks and shrubs.

104 Associated with the GPS telemetry data were the trapping data collected as part of the effort to

105 capture and deploy the collars. These data consisted of locations and nightly trap outcomes for all

106 traps and for the collared possums. Collared possums were in some cases recaptured on

107 subsequent nights. Trapping data associated with GPS collar retrieval were not included in the

108 analyses because the trapping effort was biased by using VHF telemetry to focus trap placement

109 around the known location of each possum. Trapping data included three different types of traps:

110 leg-hold traps set on the base of a tree but elevated above the ground, leg-hold traps set on the

111 ground, and cage traps. All trap types had lures deployed on them. There was no trapping data

112 associated with the GPS data for 18 collared possums. For these individuals we estimated σ but

113 not g_0. The trapping data consisted of possums captured and collared, recaptured collared

114 possums, and captured but not collared possums (which were subsequently killed).

Statistical modelling

116 We developed a hierarchical Bayesian model to make inference on factors influencing σ, g_0 and

117 population density (Fig **??**). The general approach was to use the telemetry and trapping history

118 data of the collared animals to estimate σ and g_0. Density was estimated with data augmentation

119 to identify the likely number of individuals that would go undetected given home range behavior

120 and detection probabilities (**?**).

121 *GPS location sub-model*

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122 The GPS data Z_{ijt} were composed of x_{ijt} and y_{ijt} locations for each individual i at site j at time t

123 (i.e., eastings and northings). There were L_i location fixes for individual i. We modelled the

124 probability of observing Z_{ijt} as a symmetric bivariate normal:

$$P\left(Z_{ijt}\right) = \prod_{i=1}^{L_i} Normal\left(\Delta x_{ijt}|0, \sigma_{ij}^2\right) Normal\left(\Delta y_{ijt}|0, \sigma_{ij}^2\right) \tag{1}$$

125 where σ_{ij} was the standard deviation of a normal distribution with zero mean, and Δx_{ijt} and Δy_{ijt}

126 were the distances from the home range center of individual i to x_{ijt} and y_{ijt}, respectively. The

127 home range center for each individual was calculated as the mean of all x_{ijt} and y_{ijt}.

128 We modelled σ_{ij} as a log normal with mean $ln\left(\mu_{ij}\right)$, which was a function of population density,

129 and site and individual level covariates:

$$ln\left(\sigma_{ij}\right) \sim Normal\left(ln\left(\mu_{ij}\right), E\right) \tag{2}$$

$$\mu_{ij} = \frac{K_{ij}}{\sqrt{Density_j}} \tag{3}$$

130 where E is the variance of σ, K_{ij} was a linear prediction of covariates, and $Density_j$ was the

131 estimated population density at site j (individuals ha^{-1}; see below). σ_{ij} was expected to vary

132 inversely with the square root of $Density_j$ (eq. ??; ?).

133 The predicted K_{ij} (eq. ??) determines how population density influences σ, and had the following

134 full model:

$$ln\left(K_{ij}\right) = \beta_0 + \beta_1 pForest_i + \beta_2 pScrub_i + \beta_3 pGrass_i + \beta_4 Female_i + \beta_5 Juvenile_i \qquad (4)$$

135 where *pForest*, *pScrub*, and *pGrass* were the proportion cover of forest, shrub/tussock and

136 grassland, respectively, in a 200-m radius around the home range center of each possum *i*. The

137 covariates $Female_i$ and $Juvenile_i$ were dummy variables (0 or 1) for female and juvenile possums,

138 respectively. The priors on the β coefficients and E were $Normal(0,10)$ and

139 $InverseGamma(0.01,0.01)$, respectively.

140 *Trap outcome sub-model*

141 We used the following procedure to model the trapping data $\left(Y_{ijmt}\right)$ for all N_j possums at each site

142 *j*, and across all traps *m* and nights *t*. The datum Y_{ijmt} was the trap outcome (i.e. capture or

143 non-capture) for possum *i* at site *j* in trap *m* on night *t*. These trapping data included those never

144 captured (unobserved possums). For each site and night a multinomial trial was conducted for

145 each possum, in which it could be caught in one of the M_j traps or not be captured by any trap.

146 Therefore, there were $M_j + 1$ possible outcomes for each possum per night. The probability of the

147 observed trapping data at site *j* across all individuals, traps and nights was calculated as:

$$Pr\left(Y_j|N_j,g_0,\sigma,\tau\right) = \prod_{t=1}^{T_j} \binom{N_j}{n_{jt}} \prod_{i=1}^{N_j} \prod_{m=1}^{M_j+1} \theta_{ijmt}^{y_{ijmt}} \qquad (5)$$

148 where θ_{ijmt} was the multinomial probability of the trapping outcome *ijmt*, and y_{ijmt} was a binary

149 array of length $M_j + 1$ that indicated which trap captured the possum or if it was not captured.

150 The variable n_{jt} was the number of possums captured on night *t*, and the combinatorial term

151 accounts for the number of ways that the n_{jt} possums could be caught on a given night.

152 As multinomial probabilities, the θ_{ijt} values for individual i at time t summed to one over all traps

153 and the non-capture event. These were derived by transforming the probability of capture $\left(p_{ijmt}\right)$

154 for all traps. The p_{ijmt} did not account for competition among traps to capture a possum, which

155 was incorporated into the multinomial draw of the θ_{ijmt} probabilities (eq. **??**).

156 The p_{ijmt} for the M_j traps was calculated as the following:

$$p_{ijmt} = 1 - \left(1 - \left(g_{0,ijm} e^{\left(-\frac{d_{im}^2}{2\sigma_{ij}^2} \right)} \right)^{\tau Y_{it*}} \left(g_{0,ijm} e^{\left(-\frac{d_{im}^2}{2\sigma_{ij}^2} \right)} \right)^{1-Y_{it*}} \right)^{A_{mt}} \tag{6}$$

157 where $g_{0,ijm}$ was the maximum nightly probability of capture for trap m, or the probability if the

158 trap was placed at the center of the home range of possum i (**?**). Availability status of trap m on

159 night t (A_{mt}) was set to 1 unless the trap m caught a non-target species, was sprung empty or

160 caught another possum on that night, in which case it was set to 0.5 (**?**). This reduced the

161 availability of the trap to half the night. The variable d_{im} was the distance between the home

162 range center of individual i and trap m. The τ trap-happy or trap-shy parameter was multiplied by

163 Y_{it*}, which was equal to 0 when individual i had not previously been captured by any trap, and 1

164 when it had been previously captured. A τ value < 1 would indicate that possums were trap

165 happy and would be attracted to bait on nights subsequent to being trapped, whereas τ values > 1

166 indicate that possums avoid traps on nights following the initial trapping.

167 All traps within a distance of $4\sigma_{ij}$ of individual i were considered in the calculation of eq. **??**.

168 Traps beyond this distance were considered to have a zero probability of capture. The prior on τ

169 was $Gamma(0.9333, 8.333)$ (shape and rate parameters, respectively), which has a mode of 1 and

170 variance of 0.6.

171 We predicted the values of $g_{0,ijm}$ with the following linear function:

$$logit\left(g_{0,ijm}\right) = \alpha_0 + \alpha_1 ln\left(\sigma_{ij}\right) + \alpha_2 RaisedLeg + \alpha_3 GroundLeg + \delta_i \qquad (7)$$

172 where *RaisedLeg* and *GroundLeg* were indicator variables for leg-hold traps set on the base of tree

173 and the ground, respectively. The δ_i parameter was an individual effect, and αs were covariate

174 parameters. The α_0 intercept included the effect of cage traps. The priors on the αs and δ were

175 *Normal*$(0,10)$ and *Normal*$(0,1)$, respectively.

176 We estimated *Density$_j$* as the total number of possums available to be trapped $\left(N_j\right)$ divided by the

177 effective trapping area. The effective trapping area was the area within a distance of $4\sigma_j$ from all

178 M_j traps. Unobserved possums were assigned random home range center locations within 4σ

179 meters of available traps. A possum beyond that distance would effectively have zero chance of

180 being captured, based on the half-normal detection function (eq. **??**). Each unobserved possum

181 was assigned the mean $\overline{\sigma}_j$ for site *j*, and the predicted $g_{0,ijm}$ (eq. **??**) for trap *m*. The algorithm we

182 developed sampled a large set of potential home range locations and the corresponding

183 probability of presence given the no-detection history (eq. **??**). The prior on *Density$_j$* was

184 uniform ranging from the known number of captured possums at site *j* to 20 possums ha^{-1}.

185 We assessed collinearity among the habitat covariates and did not include any two covariates that

186 were correlated with $r > |0.50|$. We explored all possible combinations of non-correlated habitat

187 variables while including *Female* and *Juvenile* in the GPS location sub-model (eq. **??**). Using

188 DIC (**?**) to compare models, we then examined the model with the most explanatory habitat

189 covariate(s) while excluding *Female* and *Juvenile*. Finally, we assessed the model with only

190 *Female* and *Juvenile* (no habitat covariates), and lastly, an intercept-only model. Preliminary

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191 analysis showed that the α coefficients for σ_{ij}, *RaisedLeg$_m$* and *GroundLeg$_m$* in the trapping

192 outcome sub-model (eq. **??**) did not overlap zero, therefore these covariates were included in all

193 models. We compared models by assessing the ΔDIC and the overlap with zero of the 95%

194 credible intervals of covariate coefficients.

195 We used Markov Chain Monte Carlo (MCMC) to estimate model parameters using the Python

196 programming language. The variance parameter E was sampled from the full conditional

197 posteriors, but all other parameters were estimated using Metropolis algorithms (**?**, pp. 175–177).

198 Posterior summaries were taken from four chains containing 3,000 samples each (total of 12,000)

199 with a burn-in of 8000 and a thinning rate of 30. Convergence on posteriors was assessed with

200 visual inspection and a scale reduction factor < 1.05 (**??**).

201 The probability of capturing or detecting a randomly located individual is the real world measure

202 of the importance on how σ and g_0 vary across individuals, populations and trapping regimes.

203 Using the posterior estimates for the model parameters, we quantified the nightly probability of

204 capture of a single possum with a randomly located home-range center in the central area of a

205 large array of traps. The array covered a large enough area so that the home range of the possum

206 was entirely within the spatial extent of the traps. This was repeated 3000 times to capture

207 parameter variability and the random location of the possum relative to trap locations. We

208 explored the effect of three trap densities (0.16, 0.58 and 2.15 traps ha^{-1}), and the three different

209 trap types (raised leg-hold, ground leg-hold, and cage traps). These trap densities correspond to

210 the following trap layouts, respectively: separation distance between trap lines equal to 400, 200

211 and 100 m; trap spacing on a line equal to 200, 100, and 50 m; and the number of trap lines equal

212 to 3, 5 and 9.

Results

Analysis of collinearity among covariates showed that *pForest* was highly correlated with *pGrass* ($r = -0.86$) and *pScrub* ($r = -0.58$). There was low correlation between *pGrass* and *pScrub* ($r < 0.12$). Given this collinearity, we first explored four models that differed by inclusion of habitat covariates, and also included *Female* and *Juvenile*: (1) *pForest*; (2) *pScrub*; (3) *pFarm*; and (4) *pScrub* and *pFarm*. Results showed that *pGrass* was the only habitat covariate that had 95% CI that did not overlap zero. The model with the lowest *DIC* had *pGrass* as the lone habitat variable and did not include *Female* and *Juvenile* (Table **??**). While the intercept-only model had the highest ΔDIC, all ΔDIC values were < 2.1 across all models.

Results of the model with the lowest ΔDIC (*pGrass* only) indicate that σ and home range size decreases with increasing proportion of productive grassland in the home range area (Table **??**). The β_0 and the *pGrass* parameters (from eq. **??**) predict the rate at which σ declines with increasing population density (eq. **??**; Fig. **??**). While σ decreased with increasing population density, there was high variability among individuals within a site (Table S1 in Supplemental Material). Home ranges tended to be smaller for females and adults than for males and juveniles, respectively; however the 95% CIs of these demographic parameters all overlapped zero.

As expected there was a strong negative exponential relationship between σ and the predicted g_0 (Fig. **??**). The rate of decrease in g_0 was highest for $\sigma < 100$ m. The predicted g_0 was highest for cage traps, followed by ground leg-hold and raised leg-hold traps, respectively (Table **??**). To illustrate the difference, for a possum with a σ of 100 m, the mean nightly probability of capture by a single cage, ground leg hold and a raised leg hold trap placed at the home range centre would be 0.151, 0.088 and 0.79, respectively. The clear superiority of cage traps over leg-hold traps goes against our expectation of the order of efficiency to be ground leg holds, raised leg holds and cage

236 traps, respectively.

237 The mean and 95% credible interval for the τ parameter were 2.05 and 1.87-2.24, respectively

238 (Table **??**). This indicated that the possums became trap shy subsequent to previous captures.

239 Despite the compensatory inverse effect of g_0 with σ, the probability of capturing a randomly

240 located possum by a large array of traps increased with increasing σ (Fig. **??**). The rate of

241 increase in the probability of capture was highest at the low range of σ, particularly with a high

242 trap density (2.15 traps ha^{-1}; Fig. **??**A). To illustrate, the mean nightly probability of capturing a

243 possum in the high density array of traps increased from 0.39 with a σ of 27 m to 0.73 with a σ of

244 100 m.

245 At the lower range of home range sizes, small increases in σ increased the potential number of

246 traps that a randomly located possum may encounter. Whereas for large home ranges there is a

247 relatively high number of traps that could be encountered, but the probability of encountering and

248 interacting with traps far from the home range center is low, resulting in the dampening of the rate

249 of increase in the probability of capture. For small σ values, the credible intervals around the

250 probability of capture are very wide because the random location of the home range center is

251 important. With small home ranges, there may be few or no traps encountered. Or, if the random

252 location was close to a trap, the combined low σ and associated high g_0 would result in a high

253 probability of capture. With high σ values the random location of the home range center is not

254 important, as all traps close to the home range center could be encountered, which drives the

255 credible intervals towards the mean capture probability.

256 The differences in g_0 for a single trap is small for the three trap types (Table **??**). However, when

257 an array of traps is deployed and a possum has the chance of being caught in one of many traps,

258 the additive effect of a more efficient trap becomes very important (Fig. **??**B). The differences in

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259 the probability of capture among trap types increases with increasing σ, because animals with

260 larger home ranges will likely encounter more traps.

Discussion

262 Estimated parameters from spatially explicit detection models have been useful in modelling

263 management and eradication of invasive animals (**????**). Selection of appropriate parameter

264 values should begin with an understanding of the ecology of the system. Our results show that

265 population density had the biggest influence on home range behaviour for possums, whereas

266 habitat had a minor effect. While some habitats are inherently more resource-rich than others, and

267 food resource availability is an important determinant of herbivore density (**???**), other factors,

268 such as population control, predators or disease, may reduce density below expected levels. For

269 invasive species such as possums in New Zealand, changes in home range behaviour following a

270 reduction in population density can occur within weeks (**?**). This presents a challenge for

271 modelling the capture/detection process of managed invasive species, particularly when

272 modelling outcomes are intended to guide management programmes spanning several years as

273 opposed to a one-off pulse of control. Stochasticity should be incorporated into the selection of σ

274 to account for uncertainty in density and for the observed inter-individual variability, which was

275 substantial in this study (Fig. **??**). The maximum probability of detection parameter (i.e., g_0)

276 should be subsequently derived from a predictive model, such as eq. **??**. Because of its inverse

277 relationship with σ, g_0 should not be drawn from a independent distribution (e.g., beta).

278 The additive effects of arrays of multiple traps magnifies the seemingly small differences in trap

279 efficiency across trap types, especially with large σs (Fig. **??**). The finding in this study that cage

280 traps were more efficient than leg-hold traps should be confirmed by further field studies. The

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281 clear superiority of cage traps over leg-hold traps goes against our *a priori* expectation of the

282 order of efficiency to be ground leg holds, raised leg holds and cage traps, respectively.

283 Three events have to occur for a trap to capture an animal, and each has an associated probability

284 of success. First, the animal has to encounter the trap, then it has to interact with it, and lastly the

285 trap has to successfully restrain the animal. The probability of animal-trap encounter should be

286 equally likely across trap types if similar lures are applied. For possums, cage traps are thought to

287 have a low probability of interaction given an encounter because the animal has to go into an

288 confined unfamiliar enclosure. Leg-hold traps can be hidden in the leaf litter (if they are not

289 raised) and are expected to have a higher probability of interaction than cage traps, but may be

290 more susceptible to miss firing and not restraining the animal. That is, cage traps may have a

291 superior probability of successful restraint given an interaction than leg-hold traps, which

292 outweighs its relatively low probability of interaction given an encounter.

293 This study and spatially explicit capture recapture studies are not able to account for animals that

294 will not interact with a trap. This risks biasing the density estimates, but our σ and g_0 estimates

295 remain robust as they were largely determined from the GPS and trapping data of detected

296 individuals. Camera traps can potentially be used to detect trap-shy individuals, since they do not

297 have to interact with the device. However, they do require the animal to approach the unfamiliar

298 device and pass through a narrow detection field. There is also the potential for camera

299 malfunction.

300 In conclusion, the application of these results to predictive modelling of invasive species should

301 differ depending on whether the objective is sustained control or eradication. Modelling sustained

302 control strategies should account for individual variability in home range size by stochastic draws

303 from the expected σ distribution (i.e. using eq. **??**; **?**). Variation in σ will subsequently influence

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304 the probability of capture of individuals (Fig. **??**) and the required trapping/detection effort.

305 Eradication operations must target the most difficult individuals to detect or remove (**?**). Given

306 the rapid increase in the probability of capture with increasing σ (Fig. **??**), the lower end of the

307 expected distribution of σ should be used for eradication attempts. When an eradication program

308 is conducted over an extended period, one might expect home range size to increase with

309 decreasing population density (**???**). However, some individuals may still maintain small home

310 range areas (i.e., individuals with low σ at low population densities; Fig. **??**), and these are the

311 ones that must be targeted in eradication operations. The cost of eradication is very high because

312 of the difficulty in removing these last difficult-to-detect individuals (**?**).

Supplemental Material

314 Data, computer scripts and detailed information on individual possums:

315 https://doi.org/10.7931/0kpk-ba78

Acknowledgements

₃₂₃ # Tables

Table 1: Study sites, predominant habitat, trap type, mean (standard deviation) of density (D, possums ha^{-1}), σ (m) and g_0. The percentage of habitat cover varied across individuals within a site (see Appendix S1 in Supplemental Material), therefore the predominant habitat may not apply to all individuals.

Site	Habitat	Trap type	D	σ	g_0
Aldinga[a,b]	Grassland	Ground leg	0.82 (0.02)	160 (48.4)	0.08 (0.04)
Muzzle[c]	Grassland	Ground leg	0.62 (0.01)	136 (72.6)	0.16 (0.13)
Catlins[d]	Grassland	Cage	1.23 (0.07)	111 (62.7)	0.15 (0.09)
Claverly[d]	Scrub	Ground leg	0.27 (0.02)	235 (47.7)	0.03 (0.02)
Leader[d]	Grassland	Cage	1.29 (0.05)	62 (5.1)	NA
McQueens Valley[e]	Forest	Cage	1.96 (0.11)	109 (38.2)	0.15 (0.09)
North Taupo 3[d]	Grassland/Forest	Cage	0.36 (0.03)	162 (70.5)	0.09 (0.05)
Orari Gorge[e]	Forest/Grassland	Cage	1.06 (0.08)	69 (15.1)	0.15 (0.04)
Puhi Puhi Peaks[e]	Scrub	Cage	3.24 (0.2)	182 (57.8)	0.07 (0.04)
Haupiri[f]	Forest	Raised leg	4.66 (0.33)	74 (28.6)	0.19 (0.08)
KmwaNonvaccine[g]	Forest	Ground leg	0.91 (0.05)	111 (42.9)	0.11 (0.07)
KmwaVaccine[g]	Forest	Ground leg	3.61 (0.20)	53 (13.7)	0.27 (0.09)
Orongorongo[h]	Forest	Ground leg	7.53 (0.41)	58 (25.6)	0.29 (0.15)
Tihoi 3A[i]	Forest	Ground leg	0.12 (0.01)	226 (21.4)	0.03 (0.01)
Waiheke[f]	Forest	Raised leg	4.64 (0.23)	93 (27.3)	0.15 (0.07)
Waikiti Hut[f]	Forest	Raised leg	4.47 (0.25)	125 (65.9)	0.11 (0.08)
Wanganui[f]	Forest	Ground leg	3.74 (0.21)	77 (24.6)	0.18 (0.08)
Whataroa[f]	Forest	Ground leg	4.82 (0.31)	78 (39.2)	0.21 (0.14)

[a] ?
[b] ?
[c] ?
[d] ?
[e] ?
[f] ?
[g] ?
[h] ?
[i] ?

Table 2: ΔDIC for models that varied in covariates in the GPS location data sub-model (eq. **??**). The trap outcome sub-model (eq. **??**) covariates of σ_{ij}, *RaisedLeg$_m$* and *GroundLeg$_m$* were included in all models.

Covariates in model	ΔDIC
pForest + Female + Juvenile	0.82
pScrub + Female + Juvenile	0.94
pGrass + Female + Juvenile	0.97
pGrass + pScrub + Female + Juvenile	1.55
pGrass	0.0
Female + Juvenile	1.42
Intercept only	2.08

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Table 3: Means and 90% credible intervals of model coefficients and associated equation numbers for the model with the lowest ΔDIC.

Coefficient	Equation	Mean	5% CI	95% CI
β Intercept	4	5.009	4.837	5.184
β *pGrass*	4	-0.170	-0.352	-0.010
E Variance of $ln\,(\sigma)$	2	1.195	1.081	1.330
α Intercept	8	5.991	4.343	7.523
α $ln\,(\sigma)$	8	-1.675	-1.978	-1.334
α Raised leg	8	-0.738	-1.271	-0.229
α Ground leg	8	-0.617	-1.024	-0.209
τ	7	2.055	1.851	2.287

Figure Legends

Figure 1 – Directed acyclic graph of hierarchical model. Data are enclosed in rectangles, estimated parameters are in ellipses and direct predictions are not enclosed. Y_{ijmt} is the trapping outcome data for possum i at site j in trap m on night t. The Z_{ijt} are the GPS location eastings and northings. The parameters at the lowest level influence the estimates of $g_{0,ijm}$, σ_{ij} and the trapping outcome data (Y_{ijmt}). Priors are not shown.

Figure 2 – The σ values (points) for 180 collared possums decreased with increasing population density. The mean predicted σ value across age-sex classes, habitat types and a range of population density values is shown with the solid black line. Vertically aligned points represent individuals from the same site and population density.

Figure 3 – The predicted g_0 values for individual possums (points) and the modelled mean (solid black line), averaged across the three different trap types and individuals.

Figure 4 – (A) The probability of capture of a single possum with a home center located randomly within a large array of traps set at three different trap densities. The g_0 was calculated using the mean value across the three trap types. (B) Using the a trap density of 0.58 traps ha^{-1}, the probability of capture of a single possum is shown for the three different trap types. The solid and dashed lines are the predicted means and 95% credible intervals, respectively.
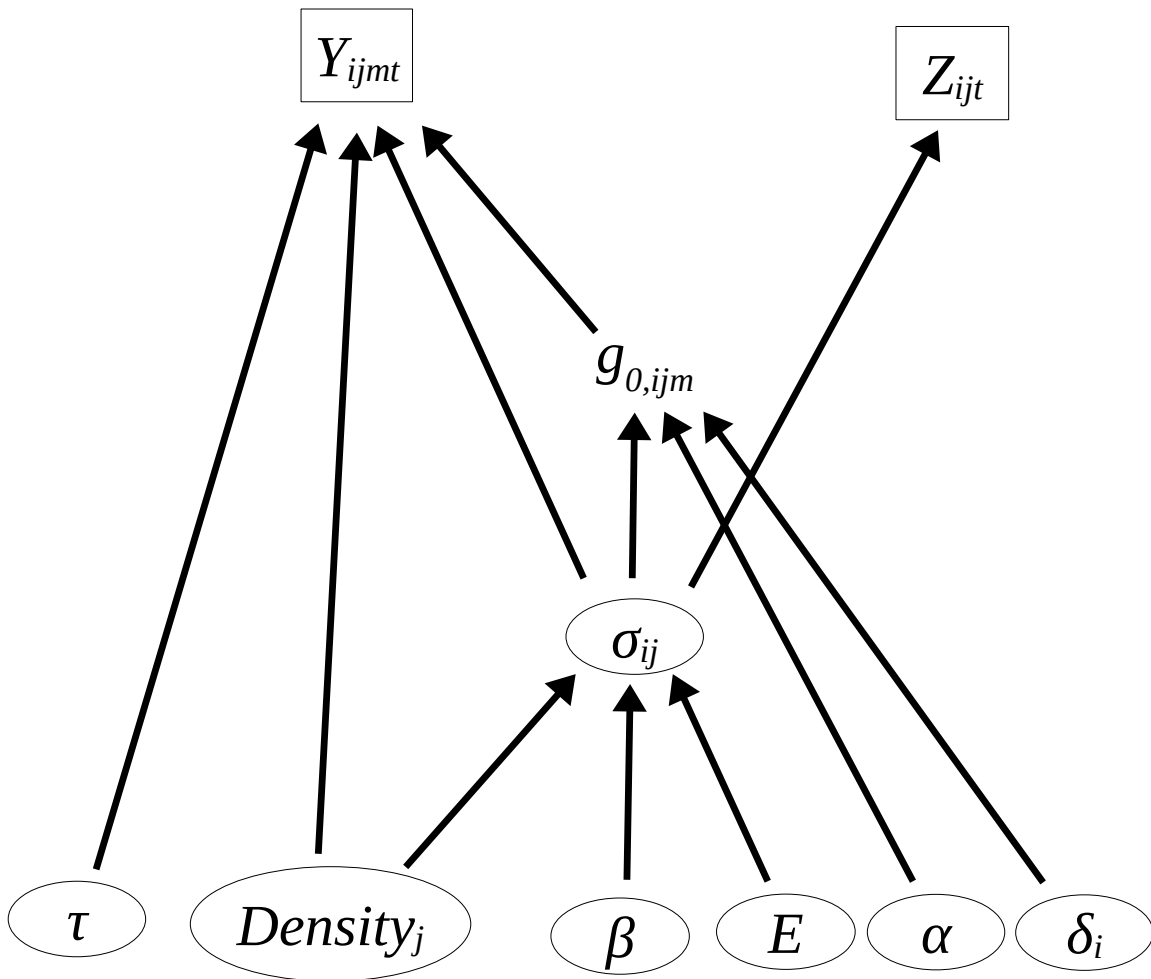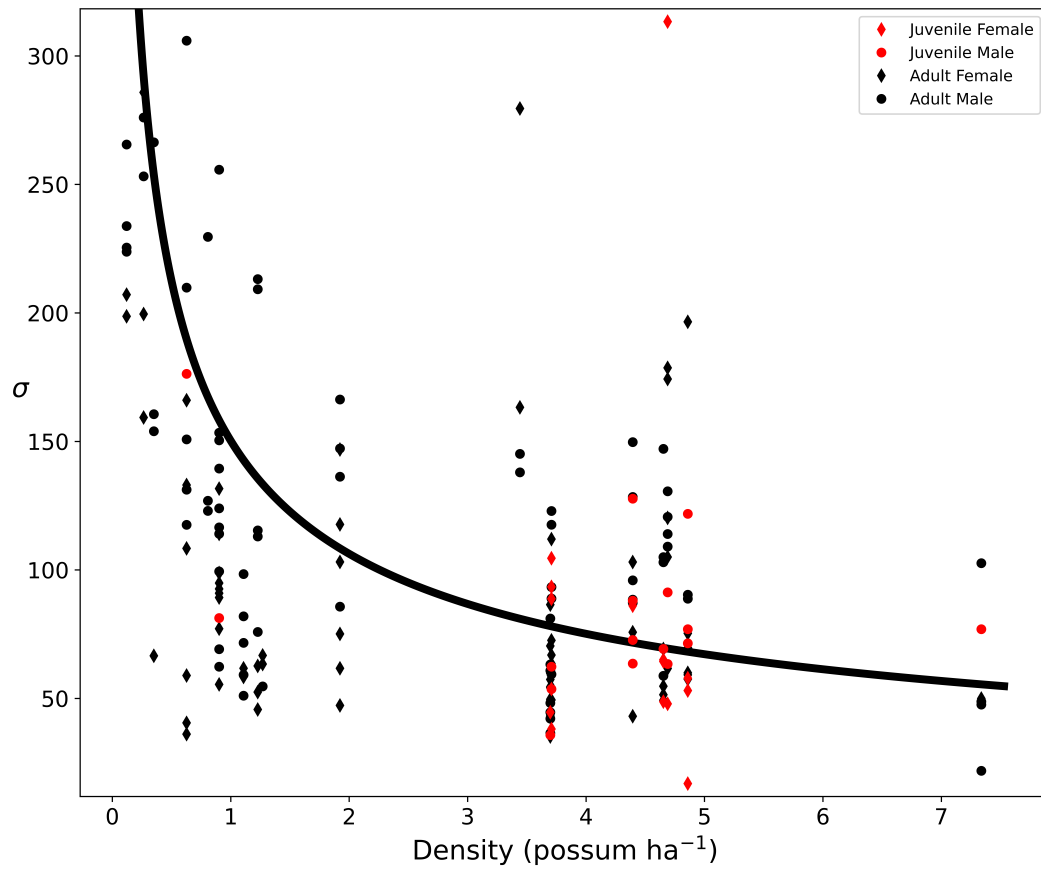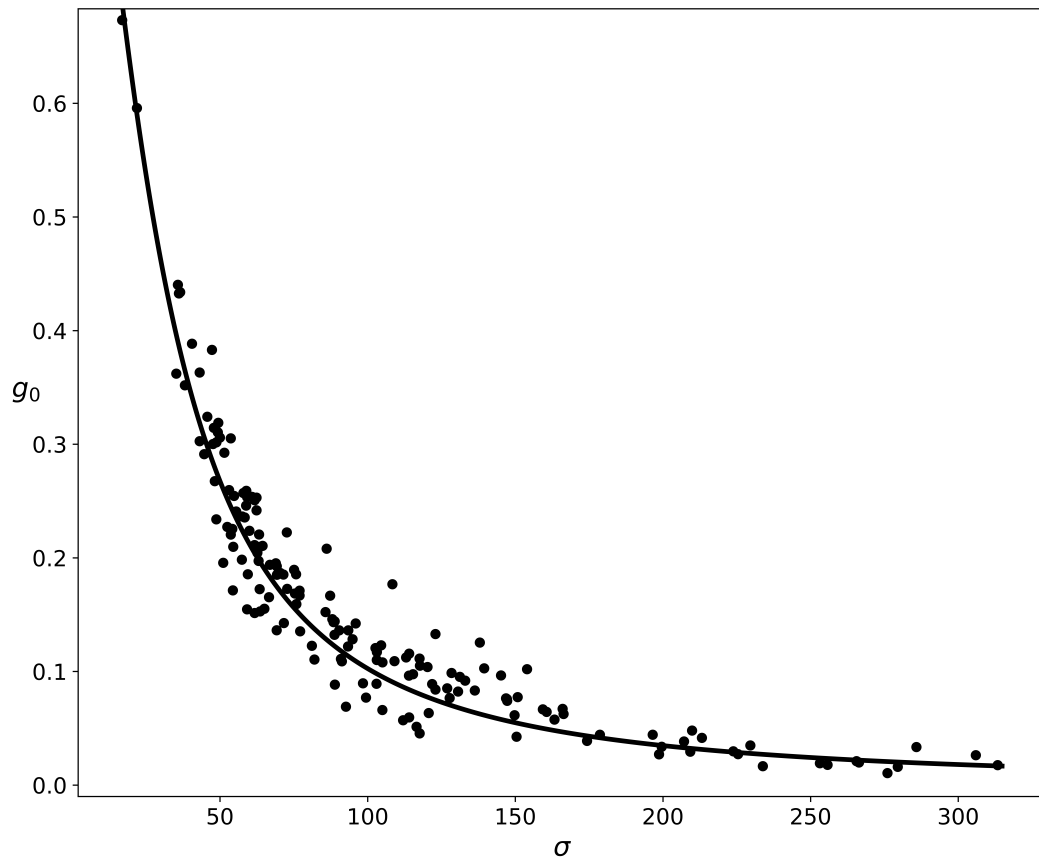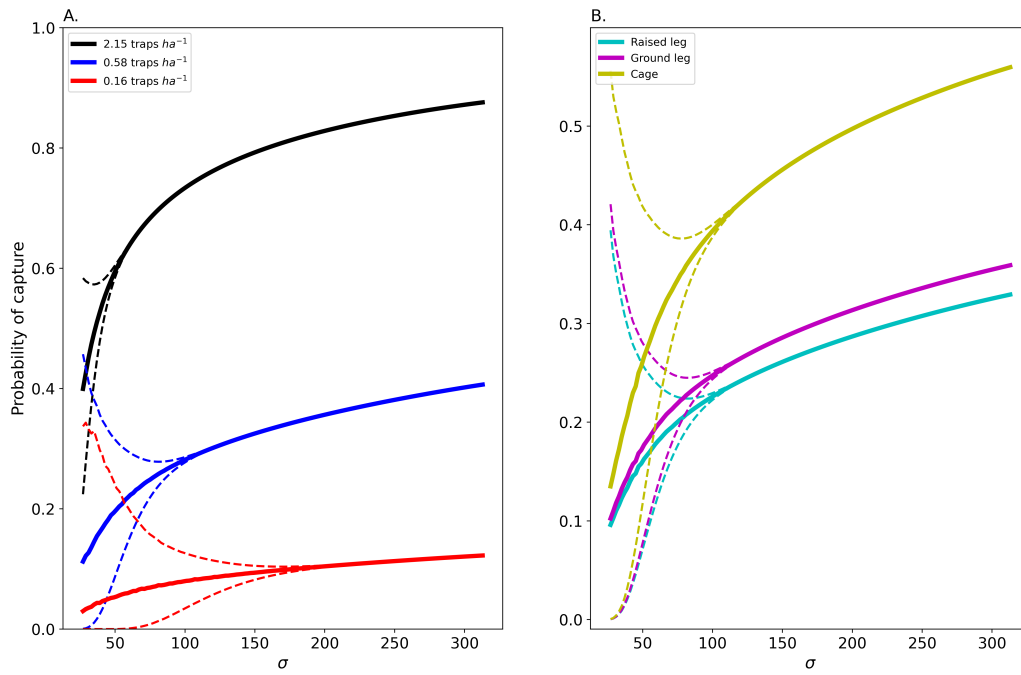
342 # Figures

Figure 1

Figure 2

Figure 3

Figure 4